UNIVERSITÉ DU QUÉBEC À MONTRÉAL

VARIATION DANS LES DÉCISIONS D'APPROVISIONNEMENT À UN POINT CENTRAL DU TAMIA RAYÉ (*TAMIAS STRIATUS*) EN PRÉSENCE DE COMPÉTITEURS

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
AMANDINE PIERRE

MAI 2006

REMERCIEMENTS

Voyez derrière ce mémoire non pas le travail d'une seule personne mais bel et bien le travail de toute une équipe qui a cru en mes capacités et qui m'a aidé à passer au travers de mes hésitations, de mes doutes et de mes angoisses. Je voudrais tout d'abord remercier deux personnes sans qui ce projet n'aurait jamais existé et avec qui j'ai pris un grand plaisir à travailler. Deux passionnés de la recherche qui m'ont appris à former mon propre esprit critique : mes directeurs Luc-Alain Giraldeau et Denis Réale. Merci à eux pour avoir décrypté mes bafouillages, respecté mon rythme, avoir été présents en tout points, pour avoir travaillé en équipe et m'avoir permis d'inclure ma vie sociale et mes passions à tout ce projet.

Parce que ses questionnements ont fait d'elle un de mes mentors, qu'elle est présente au fil de toutes ces pages et qu'elle m'a appris que "c'est la démarche qui donne tout son sens au produit final", je dédie une grande part de mes remerciements à Julie Drouin. Il y a aussi celui qui a vu naître et grandir ce projet en même temps que moi. Celui qui a eu la patience folle de m'initier au programme statistique R : Julien Martin. Je ne peux oublier toute l'équipe "Tamia" avec qui cinq mois de prise de données sur le terrain est devenue une expérience à part entière ; et tout ça grâce au ludisme de Simon Barrette, à la joie de vivre de Mélanie Dappen, à la complicité que j'ai avec Jean-Philippe Lessard, à la motivation radieuse de Chantale Falardeau et à la gentillesse de Vincent Lefebvre-Auger. Un grand merci aussi à tous ceux qui m'ont entouré dans le laboratoire : Sabrina Courant pour son impeccable organisation et pour son aide dans toutes mes démarches administratives et académiques, Kimberley-Ann Côté pour son amitié et son humour, Guillaume Rieucau et son partage naturel et pour finir merci à Phœnix Bouchard pour m'avoir encouragé à pratiquer la langue de Shakespeare. Ensuite il y a tous ceux qui font partie du GRECA (groupe de recherche en écologie comportementale et animale) avec qui les discussions étaient passionnées et passionnantes, les échanges d'opinions épiques et le café expérimental. Finalement, je voudrais remercier une deuxième fois toutes ces personnes pour m'avoir tenu compagnie pendant tous mes moments de détente autour d'une bière.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

La théorie de l'approvisionnement suppose que la sélection naturelle aurait favorisé les individus dont les décisions à propos des choix alimentaires fourniraient la meilleure aptitude. Tester les prédictions comportementales fondées sur la relation entre l'aptitude et l'efficacité d'approvisionnement demeure un des principaux objectifs des modèles d'optimalité. Le modèle d'approvisionnement à un point central concerne les animaux qui rapportent leur nourriture à un gîte. Selon ce modèle, le temps passé à amasser la nourriture d'une parcelle et donc la taille de la charge rapportée sera ajusté de manière à maximiser le taux de livraison de la nourriture au gîte. Sa prédiction qualitative, que la taille des charges rapportées augmentera avec la distance entre le gîte et la parcelle, a été mainte fois supportée chez le tamia rayé mais aucun support quantitatif n'a été apporté. La taille des charges observées était toujours plus petite que celle prédite. De plus la présence et le maintien d'une variation interindividuelle dans le comportement alimentaire des tamias ont été mis en évidence. L'existence d'un syndrome comportemental pourrait expliquer le maintien de cette variation interindividuelle. Un syndrome comportemental est une corrélation entre plusieurs comportements qui ont des effets opposés sur l'aptitude de l'animal. La corrélation génère donc des conflits de pressions de sélection entre les comportements corrélés. Dans cette étude nous verrons si chaque tamia est caractérisé par un type d'approvisionnement spécifique en observant les décisions individuelles d'approvisionnement de 24 tamias dans trois situations de compétition : absence, présence sans défense de la parcelle et présence avec défense. Dans le cas où plusieurs décisions d'approvisionnement sont corrélées, nous testerons la présence de conflits de pression de sélection en analysant l'effet de chacune des décisions sur deux indices d'aptitude : le taux d'approvisionnement et la monopolisation de la ressource. Notre étude montre que la taille des charges et le temps d'approvisionnement sont positivement corrélés et que les individus varient dans leur sensibilité à la présence d'un compétiteur. Cette corrélation apporte un support qualitatif à la prédiction du modèle d'approvisionnement à un point central au niveau individuel et chaque tamia semble être caractérisé par un type d'approvisionnement. De plus, il existe un compromis entre la taille des charges et le temps d'approvisionnement ce qui pourrait être une explication au maintien de la variation dans le comportement alimentaire du tamia rayé. Cependant, notre expérimentation ne nous permet pas de distinguer si la variation représente des décisions intrinsèques à l'individu ou des décisions dépendantes de son environnement.

Mots clefs : approvisionnement à un point central, variation interindividuelle, défense de la ressource, syndrome comportementaux, Tamia rayé.

INTRODUCTION GÉNÉRALE

L'approvisionnement regroupe un ensemble de processus par lesquels un organisme acquiert nutriments et énergie. Par le rôle essentiel qu'il joue sur la survie, la croissance ou le succès reproducteur, le comportement alimentaire a toujours attiré les écologistes évolutionnistes (Stephens et Krebs 1986, Kramer 2001). Un aspect important de ce comportement est sa plasticité phénotypique ; la capacité qu'un individu (ou génotype) a de s'exprimer de manière différente en fonction de l'environnement (Via et al. 1995, Dewitt et al. 1998). Par exemple, un animal qui s'approvisionne doit investir un certain temps en vigilance afin de détecter l'approche d'un possible prédateur. Il existe des environnements plus dangereux où les attaques de prédateurs sont plus probables qu'ailleurs. Un animal pourrait ajuster le temps qu'il alloue à la vigilance anti-prédateur selon la dangerosité des lieux, démontrant ainsi de la plasticité comportementale. Cette plasticité est vue comme une solution au problème d'adaptation évolutive à un environnement hétérogène (Via et al. 1995) et occupe donc une place importante en écologie comportementale (Stephens et Krebs 1986). Le comportement adopté par rapport aux différentes alternatives correspond à une « décision » (Kramer 2001).

Approvisionnement optimal

La théorie de l'approvisionnement suppose que la sélection naturelle aurait favorisé les individus dont les décisions à propos des choix alimentaires fourniraient la meilleure aptitude (Charnov 1976, Stephens et Krebs 1986, Giraldeau et Caraco 2000, Kramer 2001). Selon ce postulat, il devient possible de formuler des prédictions à partir de l'hypothèse que la meilleure aptitude correspond aux décisions qui maximisent le succès ou l'efficacité de d'approvisionnement. Pour faire ces prédictions il faut connaître les alternatives comportementales possibles ainsi que l'ensemble des contraintes provenant des conditions environnementales (Kramer 2001). Tester les prédictions comportementales fondées sur l'hypothétique relation entre l'aptitude et l'efficacité de l'approvisionnement demeure un des principaux objectifs des modèles d'optimalité (Stephens et Krebs 1986).

Approvisionnement social

Deux modèles d'optimalité ont été la cible de la plupart des études aussi bien théoriques qu'empiriques: le modèle des proies et celui des parcelles qui forment l'essentiel de ce que l'on nomme aujourd'hui la théorie classique de l'approvisionnement (Stephens et Krebs 1986, Giraldeau et Caraco 2000). Le modèle des proies concerne la décision d'attaquer ou d'ignorer une proie qui vient d'être détectée alors que celui des parcelles concerne la décision de poursuivre l'exploitation d'une parcelle ou de l'abandonner pour en trouver une autre (Charnov 1976, Stephens et Krebs 1986). Ces modèles d'optimalité supposent que les individus s'approvisionnent de façon indépendante et pour lesquels l'efficacité d'une décision d'approvisionnement peut s'exprimer sans devoir faire référence aux décisions des autres individus de la population. Ces modèles classiques ne s'appliquent donc qu'à des animaux présentant un type d'approvisionnement solitaire (Stephens et Krebs 1986, Giraldeau et Caraco 2000). Cependant, pour un grand nombre d'espèces, un des principaux facteurs environnementaux influençant le succès d'approvisionnement d'un individu est la présence de congénères qui engendrent de la compétition pour la ressource alimentaire (Ydenberg et al. 1986, Giraldeau et al. 1994, Lair et al. 1994, Giraldeau et Caraco 2000, Kramer 2001, Nosil 2002, Giraldeau 2005a). Lorsque c'est le cas, les méthodes traditionnelles de modélisation doivent être remplacées par des techniques qui permettent de tenir compte de la complexité des décisions et de leurs répercussions sur l'aptitude. C'est ce que propose la théorie de l'approvisionnement sociale (Giraldeau et Caraco 2000).

Compétition et défense de la ressource

L'individu qui s'approvisionne dans un contexte social se retrouve face à de nouvelles stratégies alternatives d'approvisionnement. L'animal peut réagir, par exemple, en s'engageant dans un type de « compétition par exploitation », c'est-à-dire une compétition où seule la vitesse d'approvisionnement maximise la part obtenue d'une ressource. Il pourrait tout autant faire usage de « compétition par interférence », affrontant alors de manière explicite l'adversaire, ce qui aurait pour effet de réduire la vitesse d'exploitation de la ressource des compétiteurs (Nosil 2002, Weir et Grant 2004). La compétition par interférence peut prendre

plusieurs formes : l'individu peut défendre ou tenter de s'approprier une ressource de façon agressive, avec comme conséquence une diminution du succès d'approvisionnement des compétiteurs (Getty 1981, Ydenberg et al. 1986, Grant 1993, Chapman et Kramer 1996, Civantos 2000, Kramer 2001, De Boer et al. 2003). Ces nouvelles stratégies alternatives comportementales sont bien sûr accompagnées de nouvelles contraintes. En défendant la parcelle alimentaire, l'animal peut monopoliser la ressource (Weir et Grant 2004) mais subit des coûts énergétiques et des conflits de budget temporel (Wittenberger 1981, Kramer 2001, Dubois et Giraldeau 2004). A l'inverse, une stratégie par exploitation non agressive implique une perte d'une partie de la ressource mais se traduit par moins de coûts énergétiques et temporels (Weir et Grant 2004).

Approvisionnement à un point central

La présente étude se veut une exploration de l'approvisionnement social du tamia rayé (Tamias striatus), petit rongeur diurne, solitaire et sédentaire de la famille des Sciuridae. Lorsqu'il exploite une parcelle de graines, sous la couronne d'un arbre par exemple, le tamia rayé rapporte à son terrier des graines qu'il a préalablement placées dans ses abajoues en les amassant à même la parcelle. La nourriture rassemblée et entreposée au terrier principalement à l'automne, sera utilisée pendant la saison froide (Elliott 1978). Le tamia rayé défend activement ses ressources de nourriture. Il s'éloigne rarement à plus de 45m de son terrier (Elliott 1978, Clarke et al. 1993), malgré des déplacements périodiques de plus de 100m (Elliott 1978, Giraldeau et Kramer 1982).

Le comportement d'approvisionnement du tamia rayé correspond à l'approvisionnement à un point central, une variation du modèle des parcelles classique (Orians et Pearson 1979). Ce modèle formule l'hypothèse que le temps passé à amasser les graines d'une parcelle et donc la taille de la charge rapportée sera ajustée de manière à maximiser le taux de livraison des graines au terrier. La décision du modèle des parcelles appliquée à ce scénario consiste donc à déterminer le moment auquel l'animal cessera de charger les graines d'une parcelle pour les transporter à son terrier afin de les entreposer (Orians et Pearson 1979). Le modèle suppose que le taux auquel les proies sont prises dans une parcelle diminue avec le déclin de la densité des proies de la parcelle.

De plus, le modèle suppose que le temps mis à faire l'aller-retour entre la parcelle et le terrier dépend strictement de la distance entre ces deux points. Dans ces conditions, il prédit que la taille des charges rapportées augmentera avec la distance entre le terrier et la parcelle (Orians et Pearson 1979). Plusieurs études sur le terrain ont apporté un support univoque à cette prédiction qualitative (Kramer et Nowell 1980, Giraldeau et Kramer 1982, Kramer et Weary 1991, Lair et al. 1994). Cependant, toutes ces études révèlent deux problèmes importants avec l'approche classique de l'optimalité : la taille des charges observées diffère systématiquement des prédictions quantitatives du modèle et les populations étudiées démontrent l'existence d'une variation interindividuelle importante et systématique. Il est primordial de tenir compte des conséquences de ces difficultés afin de pouvoir comprendre les forces et les contraintes sélectives qui sont responsables des comportements que nous observons. Nous proposons de tenir compte de ces deux problèmes.

Différence quantitative entre prédictions et observations

Les différences quantitatives entre la taille de charges prédites et observées pourraient provenir de ce que le modèle ne tient pas compte des dérangements occasionnés par la présence fréquente de compétiteurs sur la parcelle alimentaire (Ydenberg et al. 1986). Par conséquent, quelques attentions ont été portées pour incorporer des décisions d'approvisionnement social au model d'approvisionnement classique.

Ydenberg et al. (1986) ont modifié le model d'Orians et Pearson pour y ajouter le temps que passerait un individu à provoquer ses compétiteurs à la parcelle. Ils ont alors prédit que l'individu qui gagnerait l'exclusivité de la parcelle serait celui qui aurait les plus mauvaises options alternatives d'approvisionnement et pour lequel la parcelle contestée demeure malgré le temps perdu en compétition la seule alternative économiquement viable. Ydenberg et al. (1986) supposent alors que les comportements agressifs des tamias rayés servent plus à imposer un coût temporel au compétiteur qu'à le blesser. Les travaux de Giraldeau et al. (1994) ont apporté un support à ces prédictions en montrant que la simple présence d'un compétiteur intraspécifique dans un diamètre de 10m autour de la parcelle réduit la vitesse de chargement des graines d'un tamia. Ils notent aussi

que la présence de compétiteurs entraîne des coûts temporels supplémentaires lors de la prise de graines, augmente la vélocité lors des trajets entre la parcelle et le terrier, réduit la taille des charges et ultimement réduit le taux de charge des graines dans la parcelle. De la même façon, l'ajout d'un temps d'attente expérimental, simulant le temps d'attente dont un subordonné aurait besoin pour avoir accès à la parcelle lorsqu'un dominant est à l'intérieur, engendre des charges plus grosses chez l'individu forcé à attendre (Lair et al. 1994). Il semblerait donc que le comportement d'approvisionnement à un point central du tamia rayé n'est pas insensible à la présence de congénères. Cependant, ces études se sont contentées d'explorer l'effet de compétiteurs sur la prise de graines d'une parcelle mais elles n'ont pas étudié l'effet que peut avoir le choix du mode de compétition sur les décisions d'exploitation de la parcelle. Nous proposons donc ici de porter notre attention sur la manière dont l'usage de compétition par interférence ou par exploitation entraîne aussi des modifications importantes dans les décisions d'approvisionnement tels : la taille de la charge, le temps passé dans la parcelle et le temps passé en transit entre la parcelle et le terrier.

Variation inter-individuelle

La plupart des études du comportement d'approvisionnement du tamia rapportent l'existence de variation individuelle importante. Par exemple l'étude de Giraldeau et al. a noté cette variation pour plusieurs décisions du comportement d'approvisionnement. Une telle variation interindividuelle chez le tamia rayé a aussi été observée pour d'autres comportements. En effet, les études de Hall (2003) et de Trouilloud et al. (2004) ont observé une telle variation pour le taux de chasse, pour le taux de pauses et la durée des pauses effectuées avant de rentrer dans une parcelle. Malgré l'existence d'une grande variabilité interindividuelle pour ces différentes décisions comportementales, ces études se sont toujours concentrées sur l'effet de la valeur moyenne de ces décisions sur le succès alimentaire sans tenir compte de la variabilité. Cette persistance de la variation entre les individus sur les décisions comportementales soulève cependant une question importante. Compte tenu du rôle écologique supposé important des traits comportementaux, la variabilité de ces traits au sein d'une

population devrait subir l'aspect érosif de la sélection naturelle (Kramer 2001). En effet, la sélection naturelle favorise les traits conférant, aux individus qui les possèdent, une meilleure aptitude à propager leurs gènes aux générations suivantes (Krebs et Davies 1998), induisant une diminution de la variabilité interindividuelle de ces traits. On s'attendrait alors à ce que tous les individus de la population de tamias qui habitent un habitat aux pressions sélectives semblables, expriment leur comportement d'approvisionnement de la même façon, ce qui n'est pas le cas.

Des études telles que celles de Huntingford (1976), Riechert et Hedrick (1993), Coleman et Wilson (1998), De Boer et al. (2003) et Sih et al. (2003) ont proposé comme explication possible au maintient de la variabilité interindividuelle comportementale l'existence de syndromes comportementaux au sein de la population. Un syndrome comportemental est un ensemble de comportements corrélés entre eux (Sih et al. 2004, Sih et al. 2004a). Les syndromes comportementaux expliqueraient le maintien de la variabilité interindividuelle d'un comportement car il traduit l'existence des conflits de pression de sélection entre ce comportement et d'autres comportements associés (Sih et al. 2004). En effet, ces syndromes impliquent des corrélations entre deux comportements - ou entre deux expressions d'un comportement dans deux conditions environnementales différentes - ayant des effets opposés sur l'aptitude d'un individu (Sih et al. 2004). La sélection naturelle favorise ainsi le compromis entre deux comportements associés et explique pourquoi l'expression (ou valeur phénotypique) du comportement supposée associée à la meilleure aptitude, ne l'est pas lorsque l'on considère ce comportement de manière indépendante (Price et Langen 1992, Sih et al. 2004). Un comportement ne peut donc pas évoluer indépendamment du comportement auquel il est associé (Price et Langen 1992). Autre fait important issu du syndrome, chaque individu peut être caractérisé par un type comportemental et ne peut exprimer, pour ce comportement, toute la variation présente dans la population (Sih et al. 2004, Sih et al. 2004a). Un comportement impliqué dans un syndrome et étudié d'une façon isolée du comportement auquel il est associé, pourrait paraître mal adaptée ou sous-optimale (Riechert et Hedrick 1993, Sih et al. 2004, Sih et al. 2004a). Les situations où l'expression d'un comportement augmente une composante de

l'aptitude biologique, mais diminue d'autres composantes de cette aptitude, correspondent à des compromis (Kramer 2001). L'existence d'un compromis lorsque deux décisions sont corrélées indique l'importance de ne pas étudier ces caractéristiques indépendamment l'une de l'autre (Riechert et Hedrick 1993, Budaev et al. 1999, Sih et al. 2003 , Sih et al. 2004, Sih et al. 2004a).

Une corrélation entre deux comportements peut générer un conflit de budget temporel, ce qui amène les deux comportements à être négativement corrélés (Sih et al. 2003). C'est le cas par exemple d'une corrélation entre la vigilance et le temps d'exploitation d'une parcelle alimentaire; plus un individu alloue du temps à la vigilance, moins il exploite la parcelle. D'autres syndromes peuvent générer des conflits entre deux situations environnementales. Supposons deux situations environnementales différentes (ex : présence ou absence de congénère), dans lesquelles un comportement est observé chez plusieurs individus d'une population : la vigilance envers les prédateurs pendant l'approvisionnement. Un individu présentant un □transfert comportemental□, présentera une faible vigilance d'une façon adaptée dans la situation où il y a des congénères (c'est à dire lui conférant une bonne aptitude), mais continuera à exprimer ce comportement dans la situation où il est seul, même lorsqu'il ne confère pas la meilleure aptitude (Huntingford 1976, Riechert et Hedrick 1993, Sih et al. 2003). Lorsque ce comportement apporte, dans une situation donnée, une meilleure aptitude à l'individu, la sélection naturelle va favoriser ce comportement même s'il n'est pas adapté dans d'autres situations, ce qui peut expliquer le maintien d'un comportement mal adapté (Sih et al. 2004). Ces transferts comportementaux engendrent des corrélations positives pour une décision dans différentes situations, et peut amener des comportements à être mal adaptés à une situation (Riechert et Hedrick 1993, Sih et al. 2003, Sih et al. 2004).

Objectifs

Dans cette étude nous proposons de comparer les décisions d'approvisionnement du tamia rayé lorsqu'il est seul à une parcelle à celles qu'il montre en présence d'un compétiteur, en tenant compte de son mode particulier de compétition: compétition par exploitation ou par interférence. Nous supposons

qu'en présence d'un compétiteur, le tamia cherchera à monopoliser la plus grande part possible de la ressource contestée. Cette tentative de monopolisation peut se faire par exploitation, en évitant l'agression afin d'accroître le taux de livraison au terrier. Ainsi le tamia devrait augmenter son taux de chargement des graines à la parcelle ou augmentait la vitesse de ses allers-retours au terrier. La tentative de monopolisation peut aussi se faire par interférence, en chassant le compétiteur. Dans ce cas, le tamia devrait sacrifier son taux de livraison au terrier d'une ou deux visites mais bénéficierait au total d'une monopolisation plus élevée des ressources. Nous verrons si chaque tamia est caractérisé par un type comportemental propre en évaluant la relation qui existe entre les différentes décisions d'approvisionnement ainsi que la réponse alimentaire de chaque individu à la présence d'un compétiteur. Finalement, nous testerons la présence de conflits de pression de sélection en analysant l'effet de chacune des décisions d'approvisionnement sur deux indices d'aptitude : le taux d'approvisionnement et la monopolisation de la ressource.

ARTICLE

RESOURCE DEFENCE AND VARIATION IN THE CENTRAL PLACE FORAGING DECISIONS OF EASTERN CHIPMUNKS, *Tamias striatus*

AMANDINE PIERRE, LUC-ALAIN GIRALDEAU AND DENIS RÉALE

Département des Sciences biologiques, Université du Québec à Montréal

ABSTRACT

In this study we explore the social foraging decisions of eastern chipmunks (*T. striatus*) that carry seeds to their burrow. The central place foraging model assumes that the time taken for a round trip between the food patch and the burrow is only affected by the distance between them. In this context the model predicts that the size of the load carried to the burrow will increase with distance between burrow and central place. The eastern chipmunk has provided consistent qualitative support for the prediction, but the observed load sizes and patch times are consistently smaller than predicted values. In addition, chipmunks showed significant interindividual variation for their foraging decisions. The presence of a behavioural syndrome, a suite of correlated behaviours, has been suggested to maintain the variation between individuals for these behaviours, because the correlations between behaviours generate conflicting selection pressures. In the present study, we test whether individual chipmunks are limited in their foraging decisions by some behavioural syndromes implying the existence of distinct social foraging profiles. We tested the presence of conflicting selection pressures by evaluating the consequence of individual foraging decisions on fitness indices (the rate of food delivery and resource monopolization) in three situations of competition. Our study shows that the time taken for a round trip between the food patch and the burrow was not only affected by the distance between patch and burrow, but could also represent an individual foraging decision; a result affecting the assumption of the central place foraging model. Furthermore, individual values of load size and foraging time were positively correlated, which provides qualitative support for the prediction of the model at the individual level, and indicates a potential foraging behavioural syndrome. Each chipmunk seemed to be characterized by a specific foraging type. However, our results did not allow us to rule out whether the variation in foraging decisions was intrinsic or resulted from environmental constraints on the individual.

INTRODUCTION

Studies of foraging behaviour have highlighted the behavioural plasticity of animals, their ability to decide between alternative courses of action depending on which is the most appropriate under the circumstances (Stephens and Krebs 1986). For example, when encountering a prey item, an individual may decide to attack and eat it or instead to ignore it and search for an alternative item. These behavicural alternatives, referred to as a foraging decision, form the core of foraging theory's prey model (Stephens and Krebs 1986). This approach assumes that selection has acted to promote the maximisation of fitness returns of foraging decisions. Under this assumption optimality analysis reveals that the decision that maximises fitness returns depends on the availability of alternatives (Kramer 2001). Correctly predicting the relationships between such foraging decisions and environmental conditions provides support for this evolutionary approach to the study of behaviour known as classic foraging theory (Giraldeau and Caraco 2000). These simple optimality models have been the key to the development of the predictive study of foraging.

Classic optimal foraging models assume that individuals forage independently and hence apply mostly to solitary foragers (Stephens and Krebs 1986, Giraldeau and Caraco 2000). However, an important part of any foraging environment is often the behaviour of other foragers that may promote the expression of aggressive defence in the process of efficient acquisition of food resources (Kramer 2001, Giraldeau 2005b).

The presence of a competitor imposes new constraints that can affect an individual's foraging success and alter its optimal foraging decision. In one case an individual's optimal course of action may require that it aggressively defend the food source against all competitors. However, under other circumstances it is possible that the optimal course of action avoids the use of aggression altogether and requires instead a change of foraging behaviour that allows collection of the largest share of resources before the competitor gets it (Giraldeau and Caraco 2000). Each of these decisions is characterized by its own set of trade-offs. Defending the resource, for instance, leads to the monopolization of the resource

by the dominant (Weir and Grant 2004) but involves time budget conflicts and bioenergetics costs (Wittenberger 1981, Kramer 2001, Dubois and Giraldeau 2004). Use of a non-aggressive strategy may lead to the lost of some resources but avoids wasted time and energy related to aggression.

In this study we explore the social foraging decisions of eastern chipmunks engaged in hoarding seeds in their burrow. Chipmunks are multiple-loading central place foragers that carry loads of seeds in their extensible cheek pouches. The decision of when to stop loading at a given patch of prey and return to the central place to store the seeds has been analysed with the central place foraging model (Orians and Pearson 1979), a derivative of the now classic marginal value theorem (Charnov 1976). This model assumes that the rate at which prey are loaded is set strictly by the density of the prey within the patch. As prey density declines during loading so does the rate of prey loading. In addition, the model assumes that the time taken for a round trip between the food patch and the burrow is affected only by the distance between patch and burrow. In this context the model predicts that the size of the load carried to the burrow will increase with distance between burrow and central place. This prediction has been supported at least qualitatively by a number of experimental studies with chipmunks (see review by Kramer 2001). However, in almost every case, there remains a strong quantitative discrepancy between the observed and predicted load sizes: chipmunks consistently collect loads that are smaller than those predicted by the model (McAleer and Giraldeau in press). Ydenberg et al. (1986) argue that this discrepancy could be attributed to social factors that have not been incorporated into the classic central place foraging model. As a consequence there have been some attempts to incorporate social foraging decisions into this foraging model.

Ydenberg et al. (1986) modified the central place foraging model to incorporate interference, time wasted in challenging opponents at food patches. They predicted that individuals that gained exclusive access to a contested patch would be the ones that had the worse alternative foraging options. They assumed that aggression or threat of aggression served only to impose temporal costs rather than injuries and provided some evidence that chipmunks interfered with

each other at patches. Support for the model's predictions was provided by experimental field work of Giraldeau et al (1994) who showed that the mere presence of a competitor chipmunk within a 10 m radius of a food patch resulted in alteration of the seed loading behaviour: chipmunks collected smaller loads, had longer patch times and spent shorter times in travel when competitors were present. Similarly, Lair et al. (1994) showed that addition of experimental waiting times that simulated time that a subordinate would need to wait for access to a patch when a dominant was currently exploiting it would result in the collection of larger loads by the individual that had been forced to wait. Clearly it seemed that the central place foraging behaviour of chipmunks was not insensitive to the presence of others. In addition to the systematic observation of a significant difference between the load sizes and the patch time predicted and observed, these studies showed a significant interindividual variation for the foraging decisions (Giraldeau *et al.* 1994, Mcaleer and Giraldeau in press). Given the major role of these behaviours for an animal's fitness, one would expect that this variation would have been eroded by natural selection, and that each chipmunk would exhibit similar optimal decisions (Stephens and Krebs 1986).

Many experimental studies (review by Sih *et al.* 2004) suggested that the presence of behavioural syndromes could explain the maintenance of such interindividual variation of behavioural decisions. A behavioural syndrome is a suite of correlated behaviours (Sih *et al.* 2004, Sih *et al.* 2004a) that conflict because behavioural traits have opposing effects on fitness. In a behavioural syndrome, an individual expressing a behavioural phenotype associated with a high fitness will also express the behavioural phenotype of a second behaviour associated with a low fitness (Price and Langen 1992, Sih *et al.* 2004). Therefore, when two behaviours are correlated and conflict, different individuals can be characterized by a different behavioural type (Sih *et al.* 2004a) and a single behaviour can not evolve in isolation (Price and Langen 1992). The correlation and conflict between these behaviours can interfere with the evolution of the two behaviours towards independent optima (Sih *et al.* 2003). The existence of conflicting behavioural correlations can cause individuals to exhibit behaviour that appears suboptimal when viewed in isolation (Riechert and Hedrick 1993, Budaev *et al.* 1999, Sih *et al.* 2004, Sih *et al.* 2004a). In behavioural ecology,

conflicting selection pressures often arise because of time budget conflicts (Sih *et al.* 2003); i.e. time spent on one fitness-related activity can leave less time for another beneficial activity. The obvious consequence is that individuals cannot maximize all beneficial activities but must, instead, balance conflicting demands (Sih *et al.* 2003, Sih *et al.* 2004).

In the present study, we explore the social central place foraging further by analysing not only the patch loading decision of chipmunks but also their patch defence decision. Individuals that do not defend the resources should decrease their return time and patch time to increase their rate of food delivery in order to monopolize more food than the competitor. Whereas, individuals that chase the competitor should have a longer return time and patch time, ultimately lower rate of food delivery and higher monopolization of the resource than individuals that do not chase. We evaluated foraging decisions of individually marked chipmunks and we observed their response to the presence of a competitor. We tested the presence of a behavioural syndrome, whether chipmunks are caracterized by a individual foraging type, evaluating the relation between individual foraging decisions and evaluating the individual response to the presence of a competitor. Finally, we tested the presence of conflicting selection pressures by calculating the consequence of individual foraging decisions on fitness indices (the rate of food delivery and the degree of monopolization of the resource).

GENERAL METHODS

Study area and subjects

We carried our experiments at McGill University's Mont Saint-Hilaire Field Station, Québec, Canada, 35 km south-east of Montréal (45°33' N, 73°10' W) from May 3 to October 3 2004. The study site is a public mature beech-maple stand. Six male and 18 female chipmunks previously live-trapped, weighed, ear-tagged and fur-clipped for identification at a distance were used for the experiment. They could be used for other studies during the experimental period. All burrow entrances were located and mapped by observing individuals during hoarding (Giraldeau *et al.* 1994).

Experimental procedure

The artificial food-patch consisted of a plastic tray (45 x 30 x 5cm) containing a mixture of about 200g of sunflower seeds and 1L of vermiculite. The patch was placed haphazardly at a distance of 5 or 10m from a chipmunk burrow entrance. Once we observed the chipmunk making regular round trips we waited for one hour and placed 2-3m from the patch a video camera (digital Canon Optura) that was aimed at the patch area. We replaced the patch by an experimental patch while the chipmunk was away at its burrow. The experimental patch consisted of a similar plastic tray filled with 40g of presorted sunflower seeds (Mean ± SD, N = 50, mass = 0.14 g ± 0.03, length = 13.8 mm ± 0.79; width = 7.9 mm ± 0.74; depth = 4.2 mm ± 0.63) mixed with 1L of vermiculite. We recorded activity at the experimental patch from the videotape playbacks. Previous experiments indicated that patch depletion sets in after five to six visits to an unreplenished patch, so to avoid such depletion we limited our observations to the first three round trips to the patch.

At our study site animals can be observed from a few meters without evident disturbance (Elliott 1978, Kramer 2001). Two observers, both located near the video camera, called out behaviours into the audio channel of the video record. One observer was assigned to the focal individual and the other to the location and behaviour of any other chipmunks (referred to as competitors thereafter)

appearing within a 10m radius around the patch for more than 3 s. Each competitor was noted as being near, intermediate or distant from the patch when at 0-0.1m, 0.1-5m and 5-10m from the patch, respectively. From these data, we generated an intensity of competition index. When the competitor spent more than 80% of its time near the patch, the intensity of competition was 5. We used index values of 4, 3 and 2 when it spent more than 60% of its time between 0m and 5m, 0.1m and 5m, and 0.1m and 10m, respectively. An index value of 1 was used when it spent all its time distant from the patch. Videotapes were analysed later using Noldus Observer 4.1 as an event-recording program. The following events were recorded to the nearest 0.01s for the focal individual: arrival at the patch (all 4 paws were in the patch), departure from the patch (all 4 paws were outside the patch) and start and end of chases (the chipmunk ran briskly towards a conspecific). The number of seeds taken by both the focal individual and the competitor have been determined from video record. they «collected a seed» when their mouth removed a seed from the patch or when the seed was placed in their mouth with their forepaws.

From these events we derived six variables: 1) load size: the total number of seeds taken by the chipmunk upon leaving the patch to unload in its burrow; 2) patch time: the interval between entry and departure from the patch; 3) return time: the interval between departure and the subsequent return to the patch, including chases and the time spent in the burrow; 4) chase time: the sum of all the intervals between the start and the end of a chase by the focal animal; 5) rate of food delivery (RFD), defined as the ratio of load size over the sum of patch time and previous return time and 6) monopolization of the resource, determined by the proportion of seeds loaded by the focal individual related to the total seeds loaded by the focal individual and any competitor. Load size, patch time, return time and chase time will be considered as foraging decisions and the rate of food delivery and the resource monopolization as fitness indices (Bryant and Grant 1995, Kramer 2001, Giraldeau 2005b). We noted the competitor's identity when it was known.

Experimental design

Each round trip corresponded to one observation (a datum) and three round trips defined a session. For each chipmunk, we recorded two to three sessions at 5m and 10m from its burrow, in the presence and absence of a competitor. A total of 2 to 12 observations (mean= 3.83 ± 0.35) were recorded per chipmunk in three situations of competition: in absence of competitor, in presence of competitor without chase and with chases. Each chipmunk was observed in all three situations of competition. Observation sessions were always carried out at different locations for each distance and on different days in 73 % of cases. We carried out multiple sessions on the same day during the last month in the field to increase the number of observations per chipmunk. From late Jun until early August, we observed low above-ground activity levels. This late summer lull is commonly observed (Elliott 1978). For the temporal organization of the experiment, we divided our data in two categories: after and before the summer lull. We removed from the analysis observations during which the subject was disturbed by red squirrels, predators, humans or alarm calls.

Statistical analyses

Patch time and return time were log-transformed. Lacking sufficient observations at both distance categories to analyze them separately we standardized the behavioural variables for distance effects by subtracting each individual's data at each distance from the mean of all chipmunks at that distance and then divided this difference by the standard deviation of all chipmunks. These standardized data were then pooled for both distances.

We separated the data set into three competition situations: 1) no competitors; 2) competitor but no chase; and 3) competitor with chase. We compared the load size, the patch time, and the return time, the rate of food delivery and degree of monopolization of the focal animal between these three situations of competition using one-way ANOVAs. When we found significant differences between the three situations we could ask whether these effects corresponded to different individual foraging types or if each focal animal is able to show both foraging decisions depending on the situation. To determine which of these two cases

best describes chipmunks we ran linear mixed-models (LMMs) Restricted Maximum Likelihood on load size, patch time, return time, chase time, RFD and monopolization of the resource as a function of date (before or after the late summer lull), sex, intensity of competition (used as fixed effects), chipmunk identity and an identity*intensity of competition interaction term (used as random effects) (Nussey *et al.* 2005). We first tested the fixed effects with an F test. The fixed effects estimates represented the average plastic response to these variables for the population. Second, we tested the significance of the random effects by comparing the log-likelihood of the models with and without this random effect based on χ^2 distributed log-likelihood tests, with degrees of freedom determined by the number of additional parameters in the more complex model (Nussey *et al.* 2005).

In models with a significant random effect term, we used the best-linear unbiased predictors "BLUPs" (Nussey *et al.* 2005) to provide estimates of random effects for the variable independent of other terms within a model, standardised to a mean of zero. The BLUPs of the intercept provide a descriptor of the behavioural trait predicted by the model for each individual, in the absence of a competitor. We will refer to this value as the "baseline" behavioural trait. The BLUPs of the slope of the identity*intensity of competition interaction provide a descriptor of each individual's change in a given behavioural trait in response to an increase in competition intensity. Statistics were run using R software (Ihaka and Gentleman 1996).

Because differences between individuals have been found for each foraging decision (see results), we could ask whether these individual foraging decisions were associated with each other to test for the presence of individual foraging type. Then, we estimated the relationship between each foraging decision with a Pearson's correlation. Finally, to test for the presence of conflicting selection pressures, we determined which foraging decision most influenced the fitness indices by using a multiple regression with the BLUP values of RFD and of monopolization as a function of BLUPs of load size, patch time, return time and chase time.

RESULTS

Effect of competitors

Load size ($F_{2, 273}$ = 4.86, P = 0.0084, Fig 1a), patch time ($F_{2, 273}$ = 4.87, P = 0.0083, Fig 1b), return time ($F_{2, 273}$ = 7.70, P = 0.0006, Fig 1c), rate of food delivery ($F_{2, 273}$ = 7.38, P = 0.0008, Fig 2a) and degree of resource monopolization ($F_{2, 273}$ = 49.37, P < 0.0001, Fig 2b) were all significantly affected by the presence of competitors. Load size was larger when the competitor was either absent, or if present when it was chased (P < 0.01, Student's t test) and smallest when the competitor was present but not chased. Patch and return times were significantly longer (P < 0.05 and P < 0.01, Student's t test) and the rate of food delivery was significantly lower (P < 0.01, Student's t test) when the competitor was chased compared to when the competitor was not chased or when no competitor was present. Resource monopolization was highest in the absence of competitors (P < 0.05, Student's t test) and lowest when the competitor was present but not chased (P < 0.01, Student's t test).

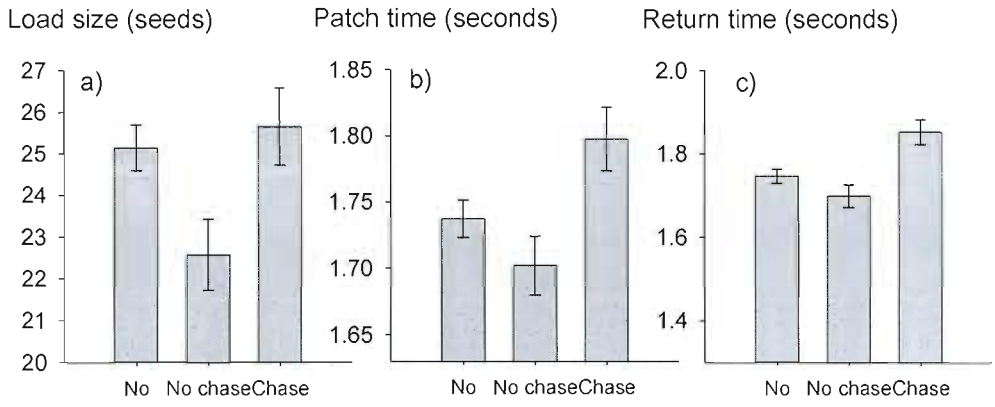

Figure 1: The relationship between the mean (±SE, N = 276) of foraging decisions (load size, patch time and return time) of 24 Eastern chipmunks in three situations of competition: No = absence of competitor, No Chase = competitor present but not chased, Chase = competitor present chased.

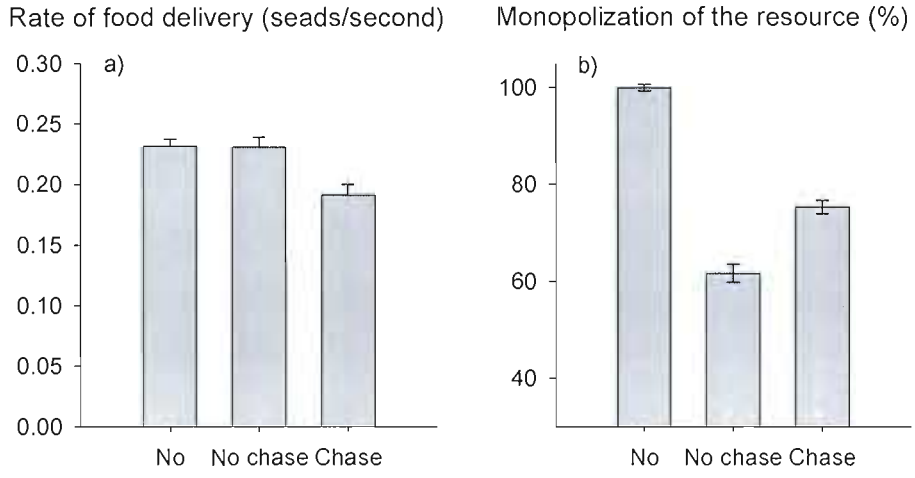

Figure 2: Relationship between the mean (±SE, N=276) of the two fitness indices (rate of food delivery and monopolization of the resource) of Eastern chipmunks in three situations of competition (for more details see figure 1).

Individual variation in response to an increase in intensity of competition

Animals adjusted their load size, return and chase times in a significantly different way when the intensity of competition increased (i.e. interaction identity*competition in Table 1, Fig 3). Some chipmunks were more sensitive to the presence of competitors than others in showing large changes in load size, return and chase times. The mean response of the population for the return and chase times both significantly increased with an increase of the intensity of competition whereas the mean response for load size and patch time were not affected (i.e. competition intensity in Table 2). Overall, monopolization and RFD significantly decreased when the intensity of competition increased (Table 2). The rate of food delivery decreased in the same way for each individual (i.e. non significant interaction identity*competition in Table 1) whereas the resource monopolization decreased in a significantly different way between individuals when the intensity of competition increased (interaction identity*competition in Table 1), with some individuals being able to maintain a higher level of monopolization than others. Patch time and return time were significantly longer and RFD lower at the end of the experimental season (i.e. date in Table 2) and sex had no significant effect on chipmunks foraging decisions and on fitness indices (Table 2).

Table 1: Log-likelihood test statistics of tree linear mixed models (LMM 1, 2 and 3) considering load size, patch time (log-transformed), return time (log-transformed), chase time, rate of food delivery and monopolization in 24 individual Eastern chipmunks experiencing variable intensity of competition. Ticks indicate differences in the random effect fitted in respective models. Differences between models were based on χ^2 distributed log-likelihood tests. Bold type in the Log-likelihood test statistic indicates significant differences between models. Bold type in the LMM indicates the selected model for generate the BLUPs. In the case of monopolization of the resource and chase time, all individuals started with the same value in the absence of competition (i.e. 0 for chase time and 100% for monopolization), and we were thus interested in testing the significance of the model with the interaction only.

		Random variables				
Variables	LMM	Identity	Identity * Competition	Log-likelihood	Log-likelihood test statistic	p-value
Load size	1			-910.7455		
	2	√		-845.6000	**130.29**	< 0.0001
	3	√	√	-837.953	**15.29**	0.0005
Patch time	1			82.11683		
	2	√		105.33761	**46.44**	< 0.0001
	3	√	√	105.6619	0.65	0.723
Return time	1			15.47808		
	2	√		26.88130	**22.81**	< 0.0001
	3	√	√	33.64447	**13.53**	0.0012
Chase time	1	√		-690.5208		
	2	√	√	-648.6443	**83.75**	< 0.0001
Rate of food delivery	1			352.7574		
	2	√		355.1903	**4.87**	0.0274
	3	√	√	356.8369	3.29	0.1927
Monopolization	1	√		42.43470		
	2	√	√	63.9997	**43.13**	< 0.0001

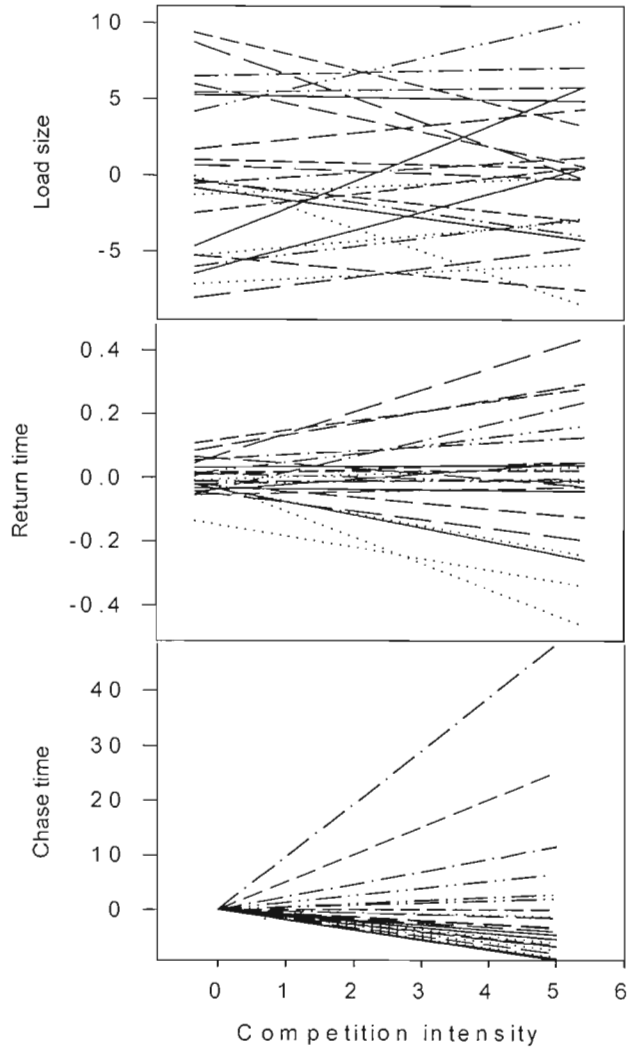

Figure 3: Mean response of each of the 24 chipmunks for load size, retrun time and chase time when the competition intensity increases.

Table 2: Results for fixed effects in the linear mixed-effect models selected on foraging decisions and fitness indices of 24 chipmunks. "Comp. Intensity" represents the increase in intensity of competition and "Date" represents two periods of observation: before and after the summer lull.

	Coefficient	F(df)	P
Load size			
Sex	-3.88 ± 2.48	2.38 (1,22)	0.14
Date	-0.20 ± 0.77	0.07 (1,250)	0.79
Comp. intensity	-0.0003 ± 0.35	0.00 (1,250)	0.99
Patch time			
Sex	-0.10 ± 0.05	1.47 (1,22)	0.24
Date	-0.09 ± 0.02	13.09 (1,250)	0.0004
Comp. intensity	0.007 ± 0.01	2.92 (1,250)	0.09
Return time			
Sex	-0.09 ± 0.05	0.39 (1,22)	0.54
Date	-0.12 ± 0.03	13.23 (1,250)	0.0003
Comp. intensity	0.03 ± 0.02	4.89 (1,250)	0.03
Chase time			
Sex	-0.13 ± 0.42	0.009 (1,22)	0.92
Date	-0.01 ± 0.33	0.02 (1,249)	0.89
Comp. intensity	1.94 ± 0.59	10.95 (1,249)	0.0011
Rate of food delivery			
Sex	-0.006 ± 0.013	3.30 (1,22)	0.083
Date	0.036 ± 0.009	14.30 (1,250)	0.0002
Comp. intensity	-0.008 ± 0.003	8.31 (1,250)	0.0043
Monopolization			
Sex	0.02 ± 0.03	0.16 (1,22)	0.70
Date	0.03 ±0.03	0.23 (1,250)	0.63
Comp. intensity	-0.18 ± 0.02	90.50 (1,250)	<0.0001

Relationships between foraging behaviours

The calculated baseline values for load size, and patch and return times were all positively correlated to each other. Chipmunks with the longest baseline values for return times also had the largest baseline values for load size and patch times (Table 3, Fig 4). Chipmunks with the largest baseline load size in the absence of competitors showed the greatest decrease in their load size when the intensity of competition increased (Table 3, Fig 5a). Chipmunks that increased their chase time the most when the intensity of competition increased also showed the highest increase in return time (Table 3, Fig 5b).

Table 3: Pearson correlations between foraging decision baselines and changes in foraging decision when the intensity of competition increases of 24 chipmunks. Individual foraging phenotypic values were obtained with the BLUPs of the linear mixed models selected. The baseline behavioural traits were obtained with the BLUPs of the intercept that provide behavioural values in absence of a competitor. The change in behavioural traits correspond to the BLUPs of the slope of the identity*intensity of competition interaction that provide a descriptor of each individual's change in a given behavioural trait in response to an increase in competition intensity. Change in patch time was not included in the analysis because there were no individual differences in the change in patch time with the intensity of competition.

	Foraging decision baseline			**Change in foraging decision**	
	Patch time	Return time	Load size	Return time	Increase in chase time
Foraging decision baseline					
Load size	0.883**	0.569**	-0.527**	0.276	0.032
Patch time	-	0.665**	-0.348	0.407	0.029
Return time		-	-0.372	0.366	0.189
Change in foraging decision					
Load size			-	0.301	0.122
Return time				-	0.478*

* $P < 0.05$ ** $P < 0.01$

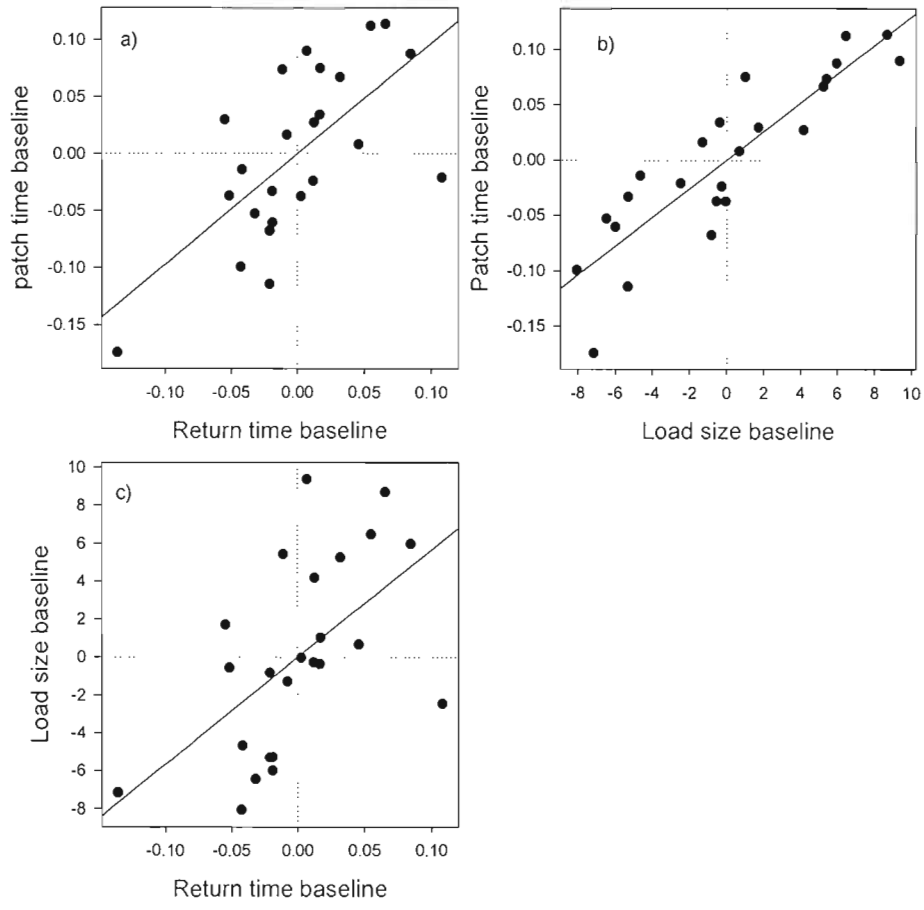

Figure 4: Correlations between load size, patch time and return time among 24 chipmunks, in the absence of a competitor (i.e. baseline).

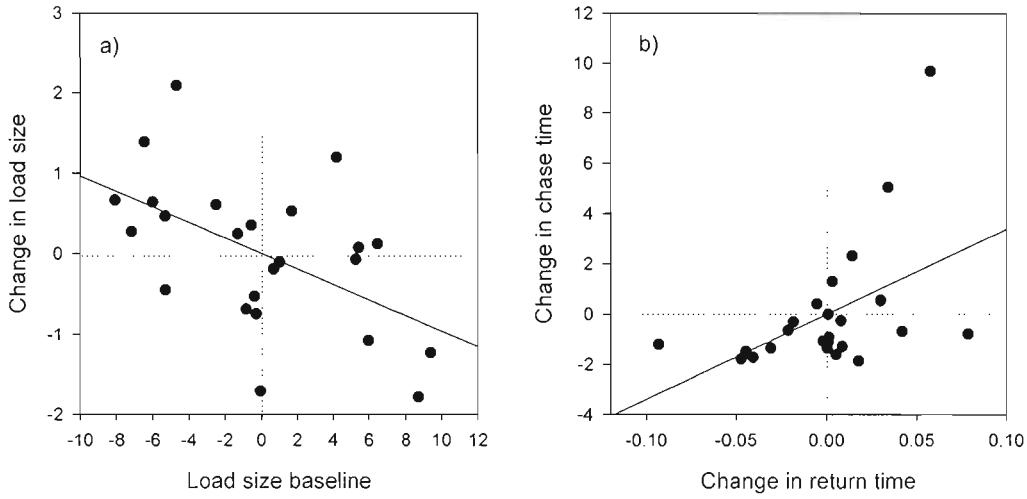

Figure 5: Correlations a) between the way in which the 24 chipmunks adjusted their load size with the increasing intensity of competition and their load size baseline and b) between the way they adjusted their return time and their chase time when the intensity of competition increased. Because BLUPs were used as predictors of change in behaviour, negative values represented values lower than the average change for that behaviour, and not automatically a negative change for that behaviour.

Influence of the different foraging decisions on fitness indices

Each foraging decision affected the rate of food delivery differently as they did on the way in which animals changed their monopolization of the resource. Increases in both baseline values for patch and return times negatively influenced the baseline values for RFD (Table 4, patch time Fig 6a and return time Fig 6b). In contrast, the calculated baseline values for RFD significantly increased with increasing load size baseline (Table 4, Fig 6c). The variance of the baseline RFD values was explained at 39% by return time baseline, at 32% by load size baseline and at 12% by patch time baseline values. When responding to the presence of competitors, an animal's change in load size, as well as return and chase times had no significant effect on the baseline values of RFD (Table 4). When responding to competition, an animal's change in load size, as well as return and chase times had no significant effect on its change in resource monopolization (Table 5). Chipmunks with the highest rate of food delivery were not the ones that showed the highest monopolization of the resource. The RFD baseline was not associated with the change of the monopolization of the resource ($r = 0.031$, $P = 0.88$, Fig 7).

Table 4: Results of a multiple regression between the baseline rate of food delivery and the foraging decisions of 24 chipmunks. The foraging decision baselines represent the foraging decisions in absence of competitor and the change in the foraging decisions represents the way in wich chipmunks adjusted their foraging decisions when the intensity of competition increased.

	Coefficient	$F_{6, 17}$	P
Load size baseline	0.003 ± 0.0005	44.21	< 0.0001
Patch time baseline	-0.12 ± 0.0358	14.50	0.0011
Return time baseline	-0.17 ± 0.0295	44.32	< 0.0001
Change in load size	0.002 ± 0.0017	0.52	0.4802
Change in return time	-0.08 ± 0.0431	0.42	0.5260
Increase in chase time	0.001 ± 0.0005	0.61	0.4462

Table 5: Results of a multiple regression between the decrease in monopolization of the resource with the intensity of competition and the foraging decisions of 24 chipmunks (for more details see table 4).

	Coefficient	$F_{6, 17}$	P
Load size baseline	0.0023 ± 0.0071	0.1026	0.7526
Patch time baseline	0.1460 ± 0.4978	0.0860	0.7729
Return time baseline	-0.1563 ± 0.4104	0.1451	0.7080
Change in load size	0.01354 ± 0.0234	0.3359	0.5698
Change in return time	-0.5835 ± 0.5982	0.9516	0.3430
Increase in chase time	0.01253 ± 0.0066	3.5850	0.0755

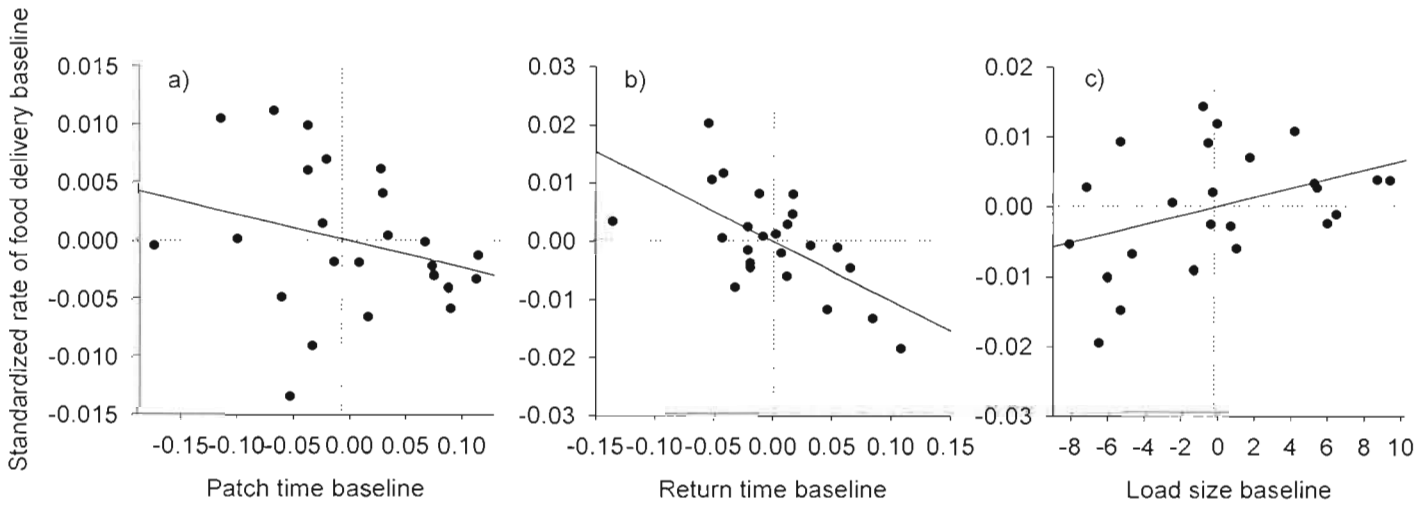

Figure 6: Linear regressions between a) rate of food delivery baseline standardized for load size and return time and patch time baseline (log-transformed), b) rate of food delivery baseline standardized for load size and patch time and return time baseline (log-transformed) and c) rate of food delivery baseline standardized for patch and return time and load size baseline.

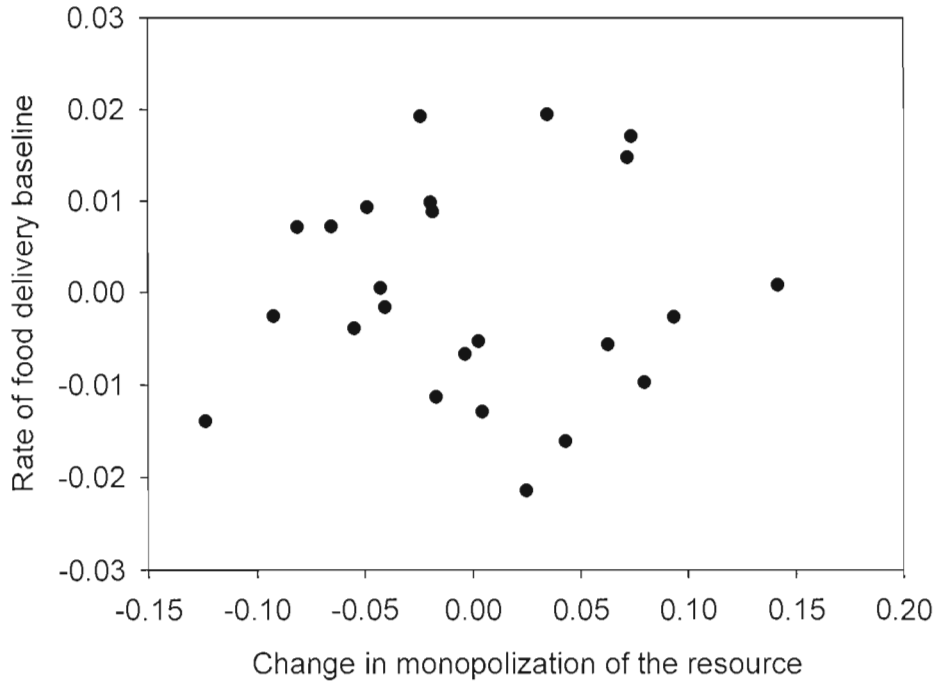

Figure 7: Relationship between the rate of food delivery baseline and the change in monopolization of the resource for 24 chipmunks.

DISCUSSION

Our study shows that the decision to defend a patch or not affects foraging decisions and fitness indices in the eastern chipmunk. As predicted, when a chipmunk forage alone, it collects large loads and its rate of food delivery is relatively high. When it decides not to chase the competitor, it takes smaller loads to its burrow, does not suffer a decline in RFD but reduces its monopolization of the ressourse. When the chipmunk chases the competitor, its load size is similar to solitar chipmunk but the temporal costs of the chase are such that its RFD declines significantly while it increase its monopolization of the ressourse. Furthermore, we found variation among individuals in their foraging decisions. In the absence of competitors, each chipmunk could be characterized by a specific set of foraging decisions. Individual values of load size, patch time and return time explained 83% of the variance in the rate of food delivery among chipmunks. Return time affected the rate of food delivery the most (i.e. 39%), followed by load size (32%). Patch time (12%) was the least important factor affecting food delivery rate. Load size increased food delivery rate, and both patch and return times decreased it. We found a trade-off between load size and both patch and return times, with animals having the higher load size also spending more time in the patch and returning. Some chipmunks appeared to be more sensitive to an increase in the intensity of competition than others. They showed higher changes than others either in load size or in return time or in chase time. This sensitivity, however, had no effect on fitness indices. Chipmunks that increased chase time the most were not the ones that had the smallest decrease in resource monopolization.

Between individual variation in foraging decisions in the absence of a competitor

There were differences among chipmunks in their baseline foraging decision. Our results therefore suggest that each chipmunk could be characterized by specific foraging decisions. Furthermore, the strong positive correlations between load size, patch time and return time at the individual level indicates a potential

foraging behavioural syndrome (Sih *et al.* 2004, Sih *et al.* 2004a); chipmunks with a longer return time had a longer patch time and a larger load size.

These results are interesting in the context of the central place foraging model (Orians and Pearson 1979). First, the positive relationship between the three foraging decisions confirms that predictions made by the central place foraging model (i.e. load size and patch time are predicted to increase with an increase in return time) are also valid at the individual level. Second, the model has always assumed that return time was the result of an extrinsic environmental constraint (i.e. the distance between the food patch and the central place) (Orians and Pearson 1979, Kramer 2001). Our results add to a growing body of evidence that return time can be viewed as a specific foraging decision and not as a result of an extrinsic environmental constraint (Giraldeau *et al.* 1994; McAleer and Giraldeau in press). It should be noted that difference in return times among individuals could still result from environmental constraints that were not measured. For example some chipmunks may occupy habitats presenting a higher level of disturbance or a higher risk of predation forcing them to spend longer in travel than others, perhaps because they have to pause more frequently than others (Trouilloud *et al.* 2004). These chipmunks should thus show longer return times and, as a consequence a larger load size and a longer patch time (Orians and Pearson 1979). Results of foraging decisions in the presence of a competitor support the hypothesis that return time can be considered a foraging decision (see below). The model should therefore take into account individual variation in return time.

Among individual variation in foraging decisions in the presence of a competitor

Competition does not affect patch time. However our results show that competition affects a number of chipmunk foraging decisions. In the case of return and chase times, competition increased the values of the traits but the reaction of some chipmunks was stronger and faster than that of others. Some chipmunks increased their load size whereas others decreased it with the intensity of competition and those that showed the highest increase had the lowest load size in the absence of a competitor. Consequently, some chipmunks

seem to be competition specialists (i.e. with the higher increase in load size) and others specialists of no competition conditions. Interestingly, because of the interaction between individuals and intensity of competition, overall load size was not affected by competition. If behavioural plasticity had not been analyzed at an individual level, load size would have appeared as a non-plastic decision when intensity of competition increased. This result reveals the importance of studying individual variation in behaviour instead of focussing on shifts in average behaviour in response to environmental variation (Sih *et al.* 2004, Sih *et al.* 2004a).

Consistent with a number of earlier studies (Giraldeau and Kramer 1982, Giraldeau *et al.* 1994, Kramer 2001) neither sex nor age seem to affect the results (One-way ANOVAs, change in load size $F_{1,22} = 0.80$, NS; change in return time $F_{1,22} = 0.80$, NS; change in chase time $F_{1,22} = 0.80$, NS). Nonetheless individuals differed in the way they reacted to increasing intensity of competition. Because we always observed chipmunks when they were close to their burrow and hence in all likelihood in a socially dominant position (Elliott 1978), this variation could not be due to differences in dominance rank of the focal chipmunks in relation to competitors.

An individual's reaction to competition may also depend on the type of competitor it is facing. Because we could not always use the same two competitors for each focal animal tested we cannot rule out that variation in behaviour we observed among individuals could be due to differences in the competitors involved with each individual. Nonetheless our results show that different individuals reacted differently to the intensity of competition, not just the identity of the competitor. This result supports the idea that the variation we observed was due to intrinsic factors and not the extrinsic local environmental conditions. More work is needed, however, to control for competitor identity.

To test the hypothesis that the variation in chase time has intrinsic causes rather than extrinsic environmental constraints, aggressiveness of each chipmunk must be observed in different environmental situations (Huntingford 1976, Riechert and Hedrick 1993, Sih *et al.* 2004). In the case of an aggression syndrome, some chipmunks will be consistently more aggressive than others (Sih *et al.* 2003, Sih

et al. 2004). For example, Riechert and Hedrick (1993) documented an aggression syndrome in a funnel web spider (*Agelenopsis aperta*) where some individuals are quicker to attack both prey and conspecific. In our study, we observed chipmunks in the context where there is only one competitor and where the arrival of food can be considered as synchronous for the focal and the competitor. Bryant and Grant (1995) showed that food was economically defendable only when it arrives asynchronously. Within a potentially aggressive syndrome, where some chipmunks are more aggressive than others, the less aggressive individual could be better off in a situation where there is only one competitor and the food arrives synchronously. Whereas the more aggressive could do best when there are many competitors and the food arrives asynchronously.

Our results indicate that chipmunks use two different strategies of resource competition: resource exploitation and resource defence (Elliott 1978). Chipmunks using the first strategy do not defend the resource. Despite the interference caused by the competitor they kept their patch and return times constant but collect on average smaller loads than when they foraged alone. These results are similar to those of Giraldeau et al. (1994), who found that at short distance (1-3m) from the burrow load sizes were smaller in the presence of a competitor than in their absence while patch and return times were constant. Chipmunks using the second strategy defend the resource by chasing the competitor, although not always successfully. As a result they increase their patch and return times but maintain their load size compared to when they are alone. With the resource exploitation strategy, a chipmunk focuses on keeping a high rate of food delivery by exploiting a higher proportion of the resource than the competitor, without preventing the competitor from gaining access to the resource. With the resource defence strategy, a chipmunk tries to monopolize a higher proportion of the resource, by chasing the competitor, but with a lower rate of food delivery than the first strategy.

Consequences of foraging and defence strategies on fitness

In this study we considered the rate of food delivery as a short-term index of fitness, because it provides a measure of the efficiency with which an individual

can bring back the highest amount of food to its burrow while spending the shortest time above ground, in a risky environment and because this has been hypothesized for chipmunks since 1980 (Kramer and Nowell 1980, Giraldeau and Kramer 1982). Among the three foraging decisions, return time had the greatest influence on the rate of food delivery; chipmunks with a shorter return time showing the higher rate of food delivery. Load size also played an important role in the rate of food delivery. Chipmunks with the higher load size showed the higher rate of food delivery. Once the effect of load size was accounted for, patch time was the least important effect on the rate of food delivery, with chipmunks spending more time at the patch showing lower rate of food delivery. Selection should thus promote chipmunks which for a given set of local environmental constraints (i.e. distance patch-burrow, risk of predation) could collect the largest load size in a minimum amount of time spent in the patch. Considering the positive correlation between the three foraging decisions and their antagonistic effects on fitness we can assume that load size, patch time and return time could not evolve independently of each other (Sih *et al.* 2004). For example selection for individuals with a shorter return time indirectly favors chipmunks with a smaller load size and a shorter patch time. None of the foraging decision combinations correspond to a higher rate of food delivery. The trade-off between return time and load size decisions may allow for the maintenance of variation of central place foraging decisions (Sih *et al.* 2004), and may explain the presence of sub-optimal foraging behaviour observed in chipmunks (Giraldeau and Kramer 1982, Giraldeau *et al.* 1994, McAleer and Giraldeau in press).

Resource monopolization, our other fitness index, was not affected by foraging decisions in the absence of a competitor. This result could be considered trivial at first sight given that monopolization of resource occurs only in the presence of a competitor. More interestingly it shows that there is no syndrome between the foraging efficiency of a chipmunk in the absence of competition and its efficiency in the presence of a competitor. We can thus reject the idea that individual chipmunks could specialize on foraging in the absence of competition or in the presence of competition.

Resource monopolization, was not affected by the adjustment in foraging and defense decisions when intensity of competition increased. The increase in the chase time by a chipmunk led to a better monopolization of the resource although not significantly (Table 4). On the other hand, we found that resource monopolization was significantly higher when the competitor was chased by the focal chipmunk. This result implies that it is the decision of chasing the competitor that increases the resource monopolization rather than the time spent chassing.

In spite of the variation in foraging decisions and their adjustment to competition, the rate of food delivery of each chipmunk decreased in the same way when the intensity of competition increased. This result and the fact that the change in foraging decisions did not affect the rate of food delivery implies that some individuals could maintain the highest rates of food delivery compared to others independently of their behavioural plasticity of foraging decisions. One possible explanation for this is that the two resource competition strategies lead to similar fitness levels; on the one hand, the exploitation strategy results in a higher instantaneous rate of food delivery than the defence strategy while the defence strategy results in a high monopolization of resources (and therefore a higher amount of resources acquired by the chipmunks) at the expense of time and energy wasted in chasing. This and a negative relationship between the two fitness indices (i.e. chipmunks that could monopolize the resource in the presence of a competitor were less efficient at bringing back the food to their burrow) would have supported the hypothesis of two separate strategies of equal fitness maintained in the population. However, we were not able to show a relationship between the rate of food delivery and the decrease in resource monopolization as a result of competition among chipmunks. It appears that some chipmunks were able both to keep a high rate of food delivery and a high level of food monopolization (i.e. the ones on the top right corner on fig 4). It is possible that our experimentation does not allow us to highlight a trade-off between the rate of food delivery and resource monopolization. In our study we observed chipmunks in the presence of only one competitor, whereas in the field it is common for chipmunks to have more than one competitor (Elliott 1978, Aniskowicz and Vaillancourt 1979). Presence of more than one competitor could generate lower rates of food delivery.

In conclusion, the present study indicates that the time taken for a round trip between the food patch and the burrow was not affected only by the distance between patch and burrow. Consequently, the central place foraging model should take into account individual variation in return time. Moreover, There is a trade-off between the load size decision and the foraging time decision indicating a potential foraging behavioural syndrome in the population. However, our experimentation does not enable us to rule out the hypothesis that the variation in foraging decisions was the result from environmental constraints rather than intrinsic .

CONCLUSION GENERALE

Cette étude nous a permis d'évaluer la différence qui existe entre les individus d'une population de tamias rayés dans leurs décisions d'approvisionnement, ainsi que la relation entre ces décisions et des indices d'aptitude. Auparavant, les études d'optimalité sur l'approvisionnement à un point central du tamia rayé mettaient en évidence cette variation sans pour autant la prendre en compte ou en saisir le sens. De plus, elles montraient que les tamias présentaient des comportements sous optimaux en abandonnant leur parcelle plus tôt et en amassant des charges plus petites que celles prédites par les modèles d'exploitation des parcelles. La variation observée entre les individus ainsi que la présence de comportements semblant sous optimaux pourraient laisser penser que chaque tamia présente un type comportemental et qu'il existe un compromis entre deux caractéristiques comportementales de l'approvisionnement. La population de tamia rayé présenterait donc un syndrome comportemental.

Notre étude valide qualitativement les prédictions du modèle d'approvisionnement à un point central au niveau individuel et montre qu'il y a des différences entre les individus dans leurs réponses à la présence d'un compétiteur. Il nous est difficile cependant de dire si la variation entre les tamias correspond a des causes intrinsèques à l'individu (ex : base génétique ou effets maternels) ou extrinsèques liées à des différences environnementales spécifiques aux individus (ex : risques de prédation autour du terrier). Chaque tamia semble caractérisé par son approvisionnement et nous avons pu mettre en évidence l'existence d'un compromis comportemental entre la taille des charges et le temps de voyagement entre la parcelle et le terrier indiquant la probable existence d'un syndrome comportemental au sein de la population. D'autre part, le temps de voyagement nous est apparu comme une décision et non comme une contrainte associée à la distance entre la parcelle et le point central. Dorénavant, les modèles devraient prendre en compte le fait que ce temps de voyagement correspond à une décision qui peut varier entre les individus.

Notre étude souligne l'importance d'étudier le comportement à l'échelle individuelle. Cependant, dans un contexte de mise en évidence d'un syndrome

comportemental, notre expérimentation présente aussi des limites. En effet, pour distinguer des causes intrinsèques aux individus de celles dépendantes de l'environnement il aurait fallu minimiser la variation entre les conditions environnementales spécifiques à chaque tamia. L'usage d'une situation de compétition, somme toute assez rare et impliquant un seul compétiteur, peut avoir limité l'expression de la défense des ressources et donc atténué la variation entre les individus quant à leur agressivité. D'autres études à plus long terme sur l'approvisionnement des tamias rayés seront nécessaires pour vérifier que cette variation inter-individuelle découle de facteurs intrinsèques à l'individu.

RÉFÉRENCES

ANISKOWICZ, B.T. and VAILLANCOURT, J. 1979. Agonistic interactions among wild eastern chipmunks (Tamias striatus). Canadian Journal of Zoology 57: 683-690.

CHARNOV, E.L. 1976. Optimal foraging, the Marginal Value Theorem. Theoretical Population Biology 9(2): 129-136.

DUBOIS, F. and GIRALDEAU, L.-A. 2004. Reduced resource defence in an uncertain world: an experimental test using captive nutmeg mabbikins. Animal Behaviour 68: 21-25.

ELLIOTT, A.L. 1978. Social behavior and foraging ecology of the eastern chipmunks (Tamias striatus) in the Adirondack Mountains of New York. Smithsonian Contributions to Zoology 265: 1-107.

GIRALDEAU, L.-A. 2005b. The function of Behavior. Dans: The behavior of animals: mechanisms, function, and evolution. Éditeurs: J.J. Bolhuis and L.-A. Giraldeau. Oxford, Blackwell Publishing Ltd. pp. 199-225.

GIRALDEAU, L.-A. and CARACO, T. 2000. Social Foraging Theory. Princeton, Princeton University Press.

GIRALDEAU, L.-A. and KRAMER, D.L. 1982. The marginal value theorem: a quantitative test using load variation in a central place forager, the eastern chipmunk, Tamias striatus. Animal Behaviour 30: 1036-1042.

GIRALDEAU, L.-A., KRAMER, D.L., DESLANDES, I. and LAIR, H. 1994. The effect of competitors and distance on central place foraging eastern chipmunks, Tamias striatus. Animal behaviour 47: 621-632.

HUNTINGFORD, B.A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, Gasterosteus aculeatus. Animal Behaviour 24: 245-260.

IHAKA, R. and GENTLEMAN, R. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical statistics 5: 299-314.

KRAMER, D.L. 2001. Foraging behavior. Dans: Evolutionary ecology: concepts and case studies. Éditeurs: C.W. Fox, D.A. Roff and D.J. Fairbairn. New York, Oxford University Press pp. 232-246.

KRAMER, D.L. and NOWELL, W. 1980. Central place foraging in the eastern chipmunk, Tamias striatus. Animal Behaviour 28: 772-778.

MCALEER, K. and GIRALDEAU, L.-A. in press. Testing central place foraging in eastern chipmunks (Tamias striatus) by altering loading functions.

NUSSEY, D.H., CLUTTON-BROCK, T.H., ELSTON, D.A., ALBON, S.D. and KRUUK, L.E. 2005. Phenotypic plasticity in a maternal trait in red deer. Journal of Animal Ecology 74: 387-396.

ORIANS, G.H. and PEARSON, N.E. 1979. On the theory of central place foraging. Dans: Analysis of Ecological Systems. Éditeurs: D.J. Horn, R. Mitchell and G.R. Stein. Ohio State, U. Press. pp. 155-177.

PRICE, T. and LANGEN, T. 1992. Evolution of correlated characters. Trends in Ecology and Evolution 7: 307-310.

RIECHERT, S.E. and HEDRICK, A.V. 1993. A test for correlations among fitness-linked behavioural traits in the spider Agelenopsis aperta (Araneae, Agelenidae). Animal Behaviour 46: 669-675.

SIH, A., BELL, A.M. and JOHNSON, J.C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution 19(7): 372-378.

SIH, A., BELL, A.M. and JOHNSON, J.C. 2004b. Reply to Neff and Sherman. Behavioral syndromes versus darwinian algorithms. Trends in Ecology and Evolution 19(12): 622-623.

SIH, A., KATS, L.B. and MAURER, E.F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. Animal Behaviour 65: 29-44.

STEPHENS, D.W. and KREBS, J.R. 1986. Foraging Theory. Princeton, Princeton University Press.

TROUILLOUD, W., DELISLE, A. and KRAMER, D.L. 2004. Head raising during foraging and pausing during intermittent locomotion as components of anti predator vigilance in chipmunks. Animal Behaviour 67: 789-797.

WEIR, L.K. and GRANT, J.W.A. 2004. The causes of resource monopolization: interaction between resource dispersion and mode of competition. Ethology 110: 63-74.

WITTENBERGER, J.F. 1981. Animal social behavior. Boston, Duxbury Press.